Interannual biomass changes and life strategies of Subantarctic zooplankton in the Kerguelen ecosystem: an overview of the consequences in energy transfer to higher trophic levels

by

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ABSTRACT. - The zooplankton communities of the Kerguelen ecosystem can be divided into the inshore, Morbihan Gulf and the shelf systems. Plankton in the Gulf displayed a high biomass and a strong seasonality with winter lows and spring and summer highs. On the shelf, the seasonality is similar but with lower levels of biomass. Zooplankton diversity is very low in the Gulf and showed an increase in species number towards oceanic waters. Energy transfer through the trophic food web was considered for the inshore system and seasonality in lipid accumulation is one of the major processes regulating the lipid availability. The main copepod, *Drepanopus pectinatus* (Brady, 1883), transforms low energy phytoplankton into high energy prey, showed high biomass and high lipid accumulation in the form of wax esters in spring and summer associated with 18:4 and 20:5 n-3 PUFA. A similar trend is observed for the copepod *Paraeuchaeta antarctica* (Giesbrecht, 1902) but because it reproduces in winter, it represents an important source of 20:5 during winter lows. The hyperiid *Themisto gaudichaudii* Guérin-Méneville, 1825 showed maximum lipid accumulation in the form of triglycerides in winter with a balanced supply of EPA and DHA (20:5 and 22:6n-3). Predation by higher predators such as fish larvae or nesting petrels showed differential predation pressure on zooplankton: fish larvae consumed essentially late stages of *D. pectinatus* while petrels fed mainly on adult stages of *T. gaudichaudii* and to a lesser extent *P. antarctica*. The main energy flow towards higher predators is well balanced between the different constituents of the zooplankton food web, but in terms of trophic upgrading and supply of essential fatty acids, *T. gaudichaudii* and *Thysanoessa macrura* G.O. Sars, 1983 appears to be the best compromise with a balance supply of both triglycerides and wax esters and high percentages of both EPA and DHA needed for the growth of most marine organisms.

RÉSUMÉ. - Changements interannuels de la biomasse et stratégies vitales du zooplancton subantarctique dans l'écosystème de Kerguelen : Vue d'ensemble des conséquences pour le transfert d'énergie vers les niveaux trophiques supérieurs.

Les communautés zooplanctoniques de l'écosystème de Kerguelen peuvent être divisées en trois systèmes: côtier, golfe du Morbihan et plateau. Une biomasse importante et une forte saisonnalité sont caractéristiques du plancton du golfe du Morbihan avec des valeurs basses en hiver et élevées au printemps et en été. La saisonnalité est identique pour le plateau mais avec des valeurs plus faibles en biomasse. La diversité zooplanctonique est très faible dans le golfe et une augmentation du nombre d'espèce est observable lorsqu'on se dirige vers les eaux océaniques. Le transfert énergétique à travers le réseau trophique a été considéré pour le système côtier et la saisonnalité dans l'accumulation de lipides s'avère être l'un des processus majeur régulant la disponibilité de lipide. L'espèce de copépode principale, *Drepanopus pectinatus* Brady, 1883, transforme le phytoplankton comportant peu d'énergie en proie à haute valeur énergétique ce qui est démontré par une biomasse et une accumulation en lipides élevées sous forme de cire au printemps et en été, associée aux 18:4 et 20:5 n-3 PUFA. Une tendance similaire est observée chez le copépode *Paraeuchaeta antarctica* (Giesbrecht, 1902) mais en raison de sa reproduction hivernale ce dernier représente une source importante de 20:5 pendant les basses valeurs d'hiver. L'amphipode hyperiide *Themisto gaudichaudii* Guérin-Méneville, 1825 montre un maximum d'accumulation lipidique sous forme de triglycérides en hiver avec un apport équivalent d'EPA et de DHA (20:5 et 22:6n-3). La pression de prédation des prédateurs supérieurs tels que les larves de poissons ou les pétrels nicheurs s'avère différente sur le zooplancton : les larves de poissons consomment plutôt les stades larvaires terminaux de *D. pectinatus* tandis que les pétrels se nourrissent essentiellement de stades adultes de *T. gaudichaudii* et, dans une moindre mesure, de *P. antarctica*. Le transfert énergétique principal vers les prédateurs supérieurs est bien équilibré entre les différents constituants du réseau trophique zooplanctonique mais, en terme de valorisation trophique et de fourniture d'acides gras essentiels, *T. gaudichaudii* et *Thysanoessa macrura* G.O. Sars, 1983 apparaissent être les meilleurs compromis de fourniture équilibrée à la fois de triglycérides et de cires ainsi qu'en pourcentage élevé d' EPA et de DHA nécessaires à la croissance de la plupart des organismes marins.

Key words. - Kerguelen - Ecosystem - Lipid transfer - Trophic food web.

Most of our knowledge of the neritic ecosystem of the Southern Ocean is derived from biological cruises around the Antarctic Peninsula and South Georgia. Far less is known on the Subantarctic lands outside of the Atlantic Sector and related marine systems. To clarify the trophic interactions between the ocean and the Subantarctic land ecosystems, interdisciplinary studies have been engaged at Prince Edward / Marion Islands (Perissinotto, 1989; Peris-

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sinotto *et al*., 1992) as well as the Kerguelen Archipelago situated close to the polar front. The offshore neighbourhood of Kerguelen has been investigated by several cruises: *Antiprod I* (Jacques, 1978), *Antiprod II* (Jacques, 1982); *Antares 2* (Fiala, 1995), *Antares 3* (Descolas-Gros and Mayzaud, 1997), *Skalp*-fisheries cruises (Duhamel, 1993) ; and the Kerfix program (Jeandel *et al*., 1998), but neritic and inlet waters remains to be described both in terms of population and processes.

This work is part of the interdisciplinary program Interaction Oiseaux- Zooplancton (IOZ), which attempts to evaluate the relationships between zooplankton as prey and as a key link in energy transfer to higher predators such as birds and fish. High latitude zooplankton is known to be a transformer of low energy phytoplankton into high energy (high lipid content) zooplankton and the main source of essential elements such as polyunsaturated fatty acids (PUFAs) (Falk-Petersen *et al*., 2009), but the importance of seasonality as well as variation in prey choice have received relatively little attention.

MATERIAL AND METHODS

Zooplankton samples were collected in Morbihan Gulf and outside with a triple-WP2 net (mesh size 200 μm) hauled vertically from 200 m, or from near bottom at the shallower stations, to the surface. Sampling was carried out inside and in the proximity of the Gulf from January 1996 to February 1997 (see Mayzaud *et al*., 2010 for details), at monthly or bimonthly intervals at different stations (Fig. 1) depending on seasons. Further sampling was done outside the Gulf at different stations along a transect northeast of the Gulf (see Blain *et al*., 2001 for details). One sample was used for biomass estimation, and one was preserved in 5% formaldehyde solution for taxonomic analysis. For biomass measurements, the plankton was transferred on to pre-weighed gauze, rinsed with a solution of ammonium formate and then frozen at -20°C. Dry biomass was estimated as the sample weight after drying at 60°C until constant weight is reached (two to three days).

Live zooplankton for lipid analyses were immediately transferred to a plastic cooler filled with surface sea water and brought back to a laboratory cold room set to *in situ* temperature. For seasonal lipid studies, groups of 200 to 300 C6 female *Drepanopus pectinatus* Brady, 1883 (with some C5 in fall and winter), 80 female *Paraeuchaeta antarctica* (Giesbrecht, 1902) and 15 adult *Themisto gaudichaudii* Guérin-Méneville, 1825 were sorted, immediately deep frozen and kept at -80°C under nitrogen and transported by air shipment to France on dry ice every three-four months.

Lipids were extracted upon arrival in France according to the method of Bligh and Dyer (1959). Lipid classes were quantified after chromatographic separation coupled with FID detection on an Iatroscan Mark V TH 10 (Ackman, 1981). Detailed methodologies can be found in Mayzaud *et al*. (2010).

Fatty acid methyl esters of each lipid class were prepared with 7% boron trifluoride in methanol according to Morrison and Smith (1964). Gas liquid chromatography (GLC) of all esters was carried out on a 30 m length x 0.32 mm internal diameter quartz capillary column coated with Famewax (Restek) in a Perkin-Elmer XL Autolab gas chromatograph equipped with a flame ionization detector. The column was

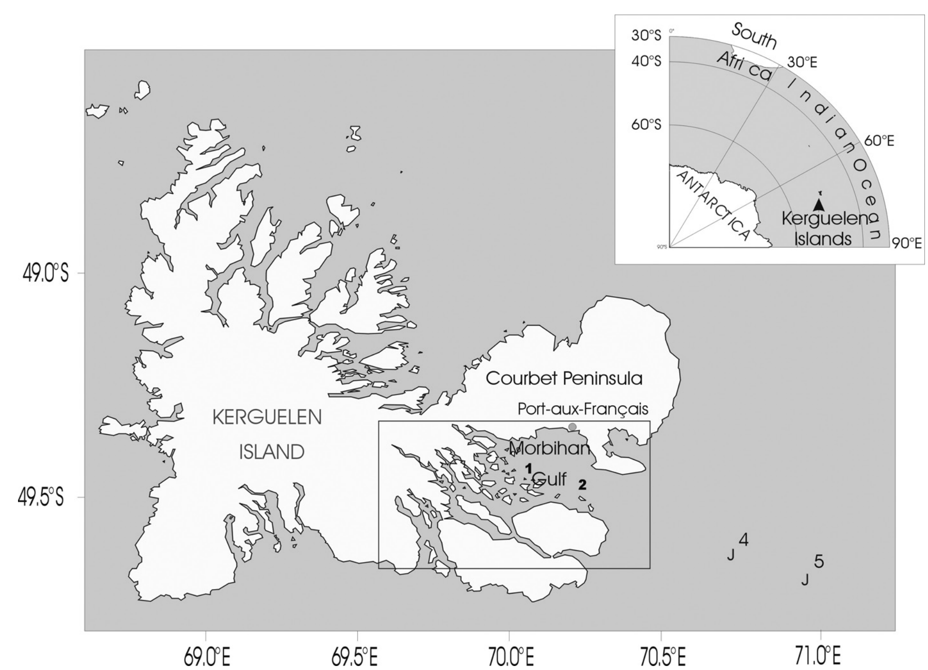

Figure 1. - Map of the location of the sampled stations inside and on the proximal shelf of Kerguelen.

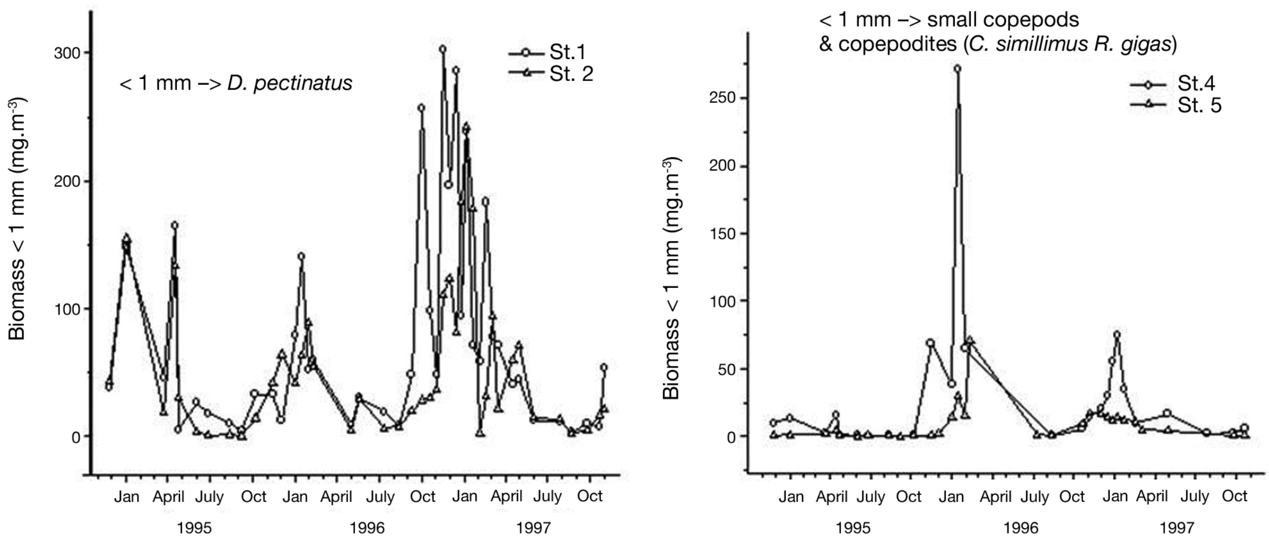

Figure 2. - Seasonal changes in the mesozooplankton total biomass inside the Morbihan Gulf (St. 1 and 2) and on the proximal shelf (St. 4 and 5) of Kerguelen.

operated isothermally at 190°C for methyl esters and 200°C for alcohol acetates. Helium was used as carrier gas at 7 psig. The injector and detector were maintained at 250°C. Individual components were identified by comparing retention time data with those obtained from authentic and laboratory standards. In addition to the examination of esters as recovered, a part of all ester samples was completely hydrogenated and the products examined qualitatively and quantitatively by GLC. The level of accuracy was ± 5% for major components, 1 to 9% for intermediate components and up to ± 30% for minor components.

Stomach content from seabirds and fish larvae was estimated as described by Bocher *et al*. (2000) and Koubbi *et al*. (2009). In brief, total numbers of items were counted in each individual sample. Prey species were identified using published keys and our own reference collection. Thirty to 60 items (either intact specimens and/or intact eyes) of the main crustacean prey were randomly selected and measured per dietary sample. In order to estimate the composition by mass of the diet, the body mass of crustaceans, fish, cephalopods and other organisms was estimated from body length using published relationships and our own equations. The reconstructed mass of each taxon for each sample was calculated from the average wet body mass for the species in the sample. The value was then multiplied by the number of individuals in the sample, and the resulting value was pooled with those calculated for the same taxon in the other samples. The calculated masses for all the different taxa were then pooled, and the reconstituted proportion by mass of each taxon then calculated as the percentage it represented in the total reconstituted mass.

RESULTS

Interannual changes in zooplankton biomass and population structure

In the inner part of the Gulf, changes in zooplankton biomass showed a strong seasonality, across all stations considered (Fig. 2). Highest biomass was observed during the summer periods while winter displayed lowest values. Although the seasonal cycle showed a similar pattern during all three years of the survey, interannual variability was also recorded. Indeed, while 1995 and 1996 showed similar ranges of values, with maxima of 200 mg m^{-3}, 1997 showed a higher

Table I. - Zooplankton species composition at different stations inside and outside Morbihan Gulf (see Blain *et al*., 2001 for station location).

Kerguelen shelf October 1995	Ind/m^3 (% total)			
Stations # (isobath)	2 (100 m)	3 (200 m)	10 (2000 m)	14 (3000 m)
Calanus simillimus	0.16	0.48	4.58	3.69
Clausocalanus laticeps	0.01	0.05	0.21	0.46
Ctenocalanus citer	1.60	8.14	25.13	42.26
Drepanopus pectinatus	65.02	19.48	11.55	0.08
Oithona frigida	14.79	48.02	16.98	18.78
Oithona similis	18.27	23.48	34.64	24.82
Pareuchaeta (copepodites)	0.00	0.00	2.38	0.21
Rhincalanus gigas	0.03	0.03	2.29	3.52
Pteropods	0.01	0.05	0.42	4.40

secondary production with maximum biomass exceeding 300 mg m^{-3}. The pattern recorded outside at close proximity of the mouth of the Gulf displayed lower biomass values and the seasonal signal attenuated with distance from the Gulf (Fig. 2). Interestingly, 1996 displayed maximum values on the proximal shelf rather than 1997 as recorded inside the Gulf. Splitting the biomass by size fraction revealed that the largest component was comprised of the smaller size fractions. Inside the Gulf, the seasonal changes of zooplankton was dominated by the < 1 mm fraction, the copepod *D. pectinatus*. Outside the Gulf, the changes were dominated by small copepod species (< 1 mm) and copepodite stages of *Calanus simillimus* Giesbrecht, 1902 and *Rhincalanus gigas* Brady, 1883. The larger size range (> 3 mm) encompasses large copepod species, euphausiid and hyperiids but always represented a small fraction of the biomass.

Detailed taxonomic composition of the zooplankton community of the Kerguelen shelf area was carried out for the early spring period over a transect from the entrance of the Gulf towards the shelf break (Tab. I). As expected, the small copepod species (*Oithona* spp.) were an important contributor in numbers to the community structure at all stations. However, the station close to the entrance of the Gulf was dominated by the copepod *D. pectinatus*, with it's contribution decreasing drastically towards the offshore waters. Conversely, species such as *Ctenocalanus citer* Heron and Bowman, 1971, *C. simillimus*, *R. gigas* or pteropods showed increasing importance in more oceanic waters.

Seasonal changes in lipid and fatty acid supply from copepod prey to higher consumers

The energy transfer from secondary producers to higher predators was considered within the Morbihan Gulf community. The complexity of the community structure and interactions of the hydrodynamic features made it difficult to resolve the situation for the entire shelf system. Hence we will consider the main three species constituting the Gulf population: the copepods *D. pectinatus* and *P. antarctica* and the hyperiid *T. gaudichaudii*.

Seasonal changes in lipids of Drepanopus pectinatus

Dry weight of C5-adult stages showed maximum values in spring and summer (Fig. 4) following the periods of increased phytoplankton abundance. Changes in dry weight were significantly correlated with changes in total lipid content ($F_{1,27} = 12.18$, $p = 0.0017$), which displayed similar seasonal pattern with summer high and winter low concentra-

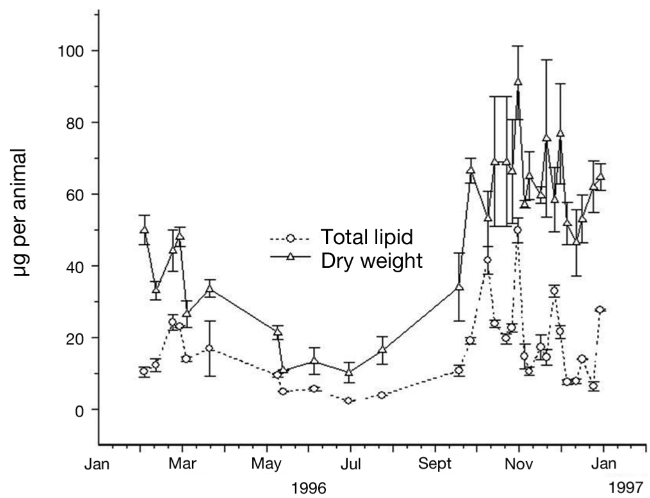

Figure 3. - Seasonal variations of *Drepanopus pectinatus* adult female dry weight and lipid content per individual.

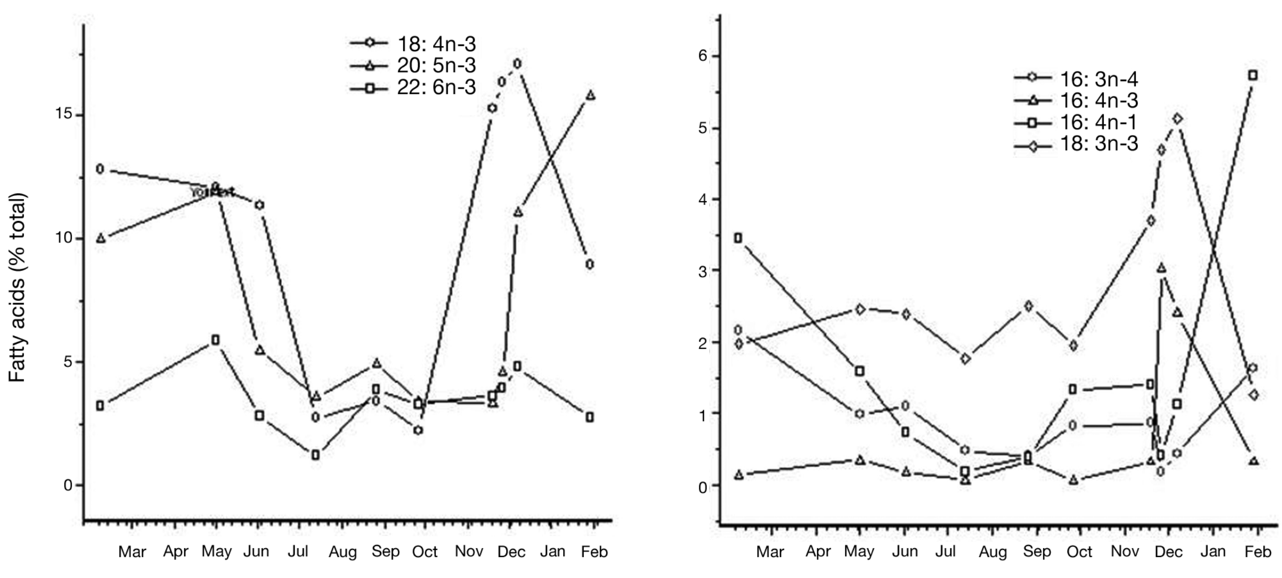

Figure 4. - Seasonal changes in the PUFA composition of *Drepanopus pectinatus* females.

tions (Fig. 3). These changes were associated with changes in size, with maximum values in spring-summer and minimums in winter.

The fatty acid composition of wax esters (WE) dominated at all times (Fig. 4). Polyenes with 4 double bonds were the dominant PUFA fraction with 18:4n-3 ranging from less than 3% in winter and interesting high levels of 10% during spring and summer. Substantial amount of 20:5n-3 (10-15%) was recorded during summer while smaller, but significant, amounts of 16:4n-1 was abundant in summer. Dienoic acids were essentially 16:2n-4 and 18:2n-6 while trienoic acids were dominated by 16:3n-4 and 18:3n-3. The changes in n-3 PUFA showed marked seasonal changes with a decreasing trend in fall, minimal values in winter and increasing percentages throughout spring and summer. Minor PUFA included 16:3n-4, 16:4n-3, 16:4n-1, 18:3n-3. They are considered as diet markers and followed the changes in the diatom spring and summer blooms.

Seasonal changes in lipids of Paraeuchaeta antarctica

The changes in dry weight and total lipid content are described in detail by Alonzo *et al*. (2000). We will focus on the availability of PUFA in relation to population abundance and reproductive cycle. In terms of population structure *P. antarctica* showed the usual summer maximum in abundance and winter minimum (data not shown). However, as shown by Alonzo *et al*. (2000), the summer population is dominated by young copepodites while the winter ones are characterized by the recruitment of reproducing females (up to 40% of the population).

Lipid content of females was dominated by wax esters with minor contribution of polar lipids and triglycerides (Fig. 5). The main feature of the seasonal cycle is a drastic reduction in wax esters during the winter month in relation with the reproductive period. The inverse changes of triglycerides are interesting as they suggest a shift in the energy requirements during reproduction.

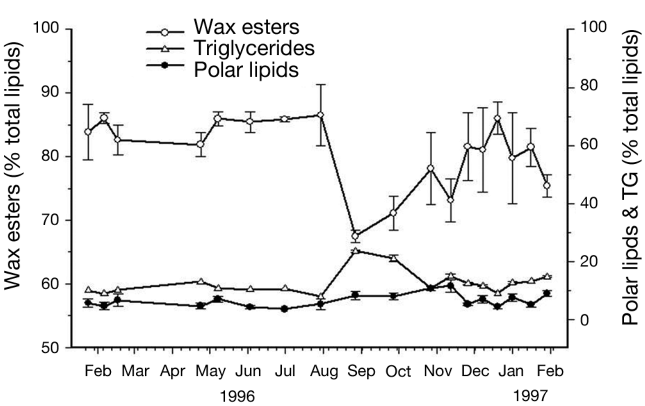

Figure 5. - Seasonal changes in lipid class composition of *Paraeuchaeta antarctica* females.

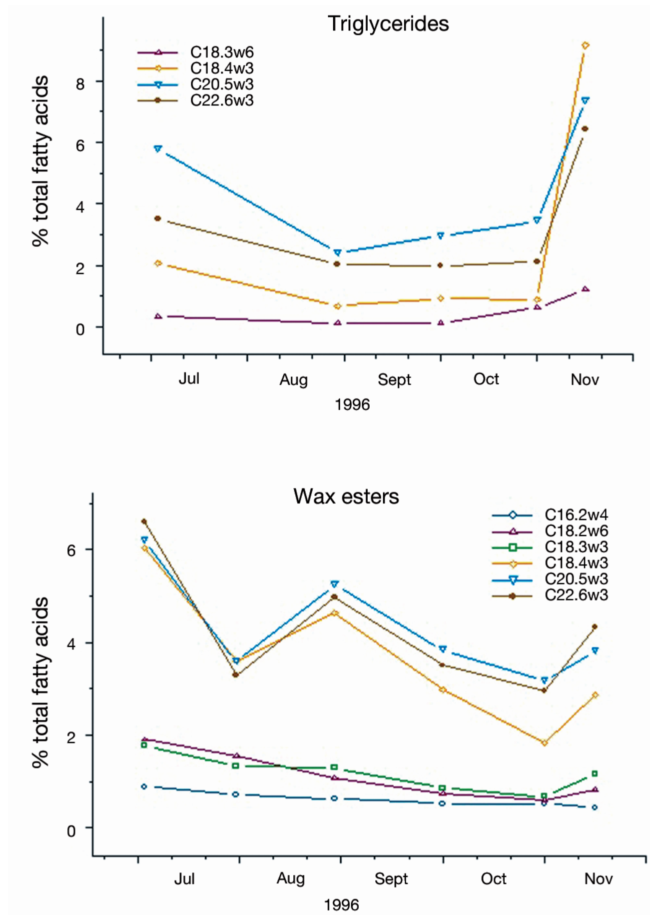

Figure 6. - Changes in PUFA constituents of wax esters and triglycerides during the winter period of reproduction of *Paraeuchaeta antarctica*.

Considering the variation in PUFA content of both wax esters and triglycerides during the reproduction, it appears that most wax esters PUFA are heavily used throughout the winter and early spring period (Fig. 6). Similar changes are present with the triglycerides but recovery of PUFA percentages occurred as early as October, i.e. early spring.

Seasonal changes in lipids of Themisto gaudichaudii

Changes in dry weight and lipid content per individual followed those recorded for *P. antarctica*, i.e., low winter values and maximum summer ones (data not shown). When computed on a % dry weight basis, changes in total lipids clearly showed low percentages in spring during the breeding season and maximum in winter (Fig. 7). Contrary to the two copepod species studied, lipids are dominated most of time by the phospholipid fraction while neutral lipids consisted of triglycerides and to a lesser extent wax esters (data not shown). For reproduction, *T. gaudichaudii* seems to draw its energy requirements essentially from the triglyceride fraction and complement with wax esters. Consequently,

the (n-3) PUFA were differentially used throughout spring (Fig. 8), while wax esters PUFA percentages decreased earlier (mid winter) and recovered as early as mid-spring. This suggests two different roles: triglycerides supplying the reproductive needs while wax esters supported the winter survival requirements.

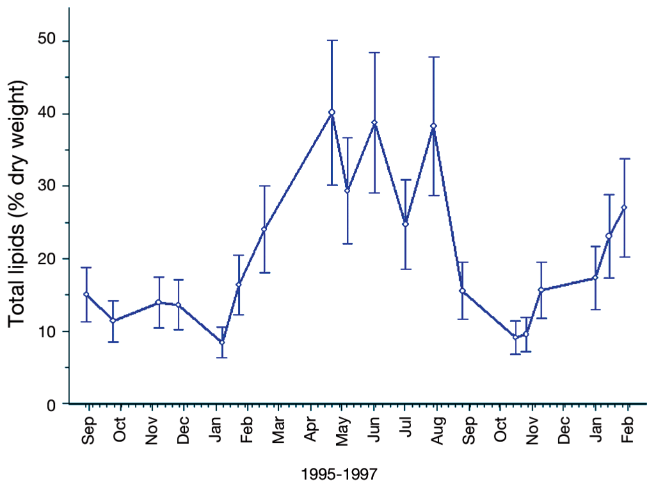

Figure 7. - Seasonal changes in total lipid of *Themisto gaudichaudii* adults.

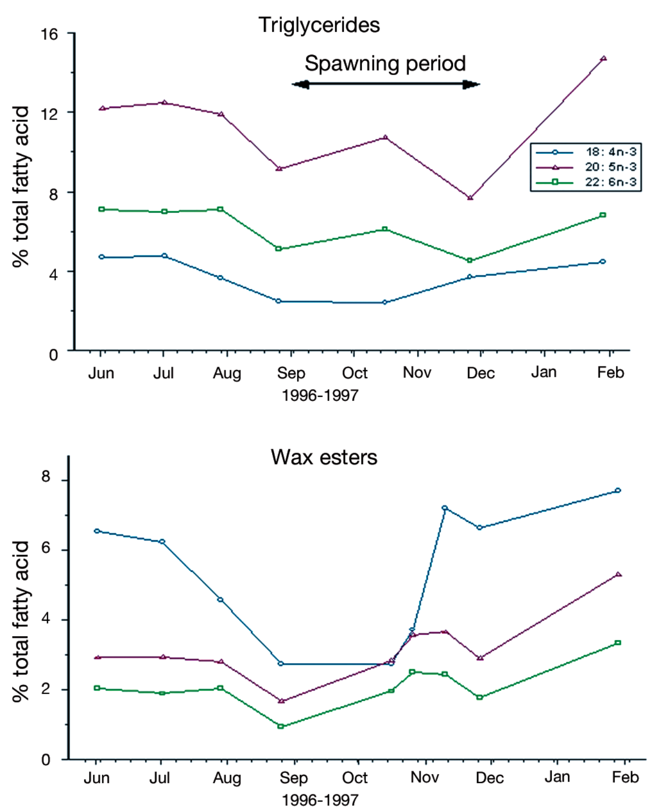

Figure 8. - Changes in PUFA constituents of triglycerides and wax esters of *Themisto gaudichaudii* during the winter and spring periods.

Trophic interactions of higher predators

Seasonal changes for Notothenia cyanobrancha *larvae*

In coastal environment, fish larvae remain one of the main zooplankton predators. In the context of Morbihan Gulf it can be seen that diet of *Notothenia cyanobrancha* Richardson, 1844 varies with time following the abundance of the different prey (Fig. 9). In winter when biomass is lowest, the larvae feed on a relatively large spectrum of prey with *D. pectinatus* as the main item but with significant contribution of tintinnids, *C. simillimus,* harpacticoids and various copepod nauplii. In spring, the contribution of *D. pectinatus* to the diet increases but is complemented by various nauplii. In summer, more than 80% by mass of the diet is composed of *D. pectinatus* with a small contribution of harpacticoids.

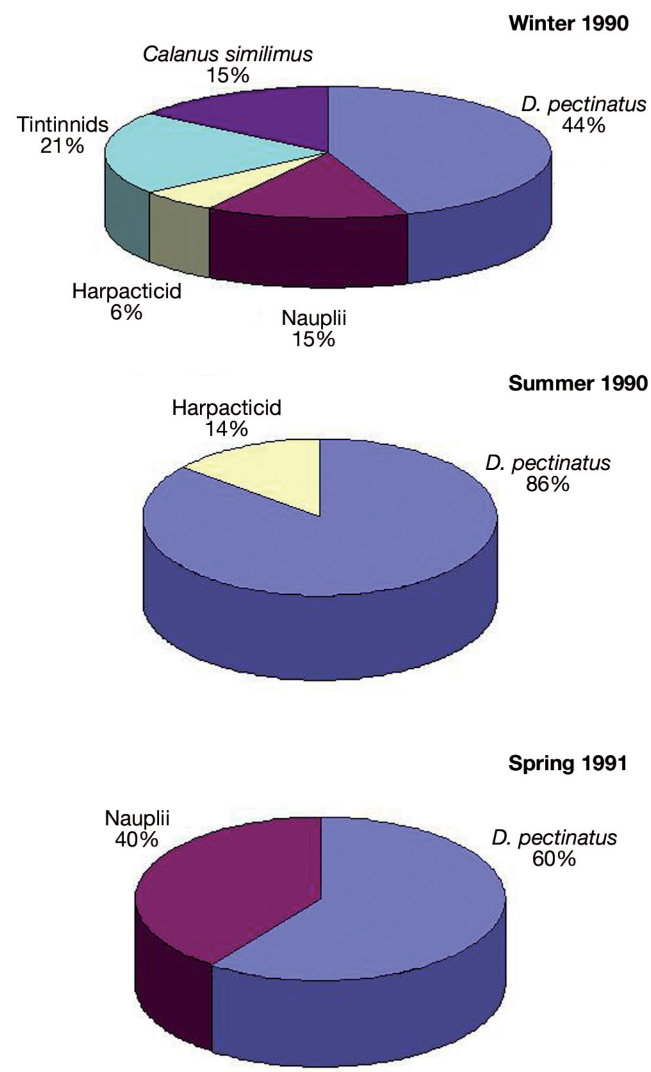

Figure 9. - Stomach content (% mass) of larval stages of *Notothenia cyanobrancha* (notothenid fish).

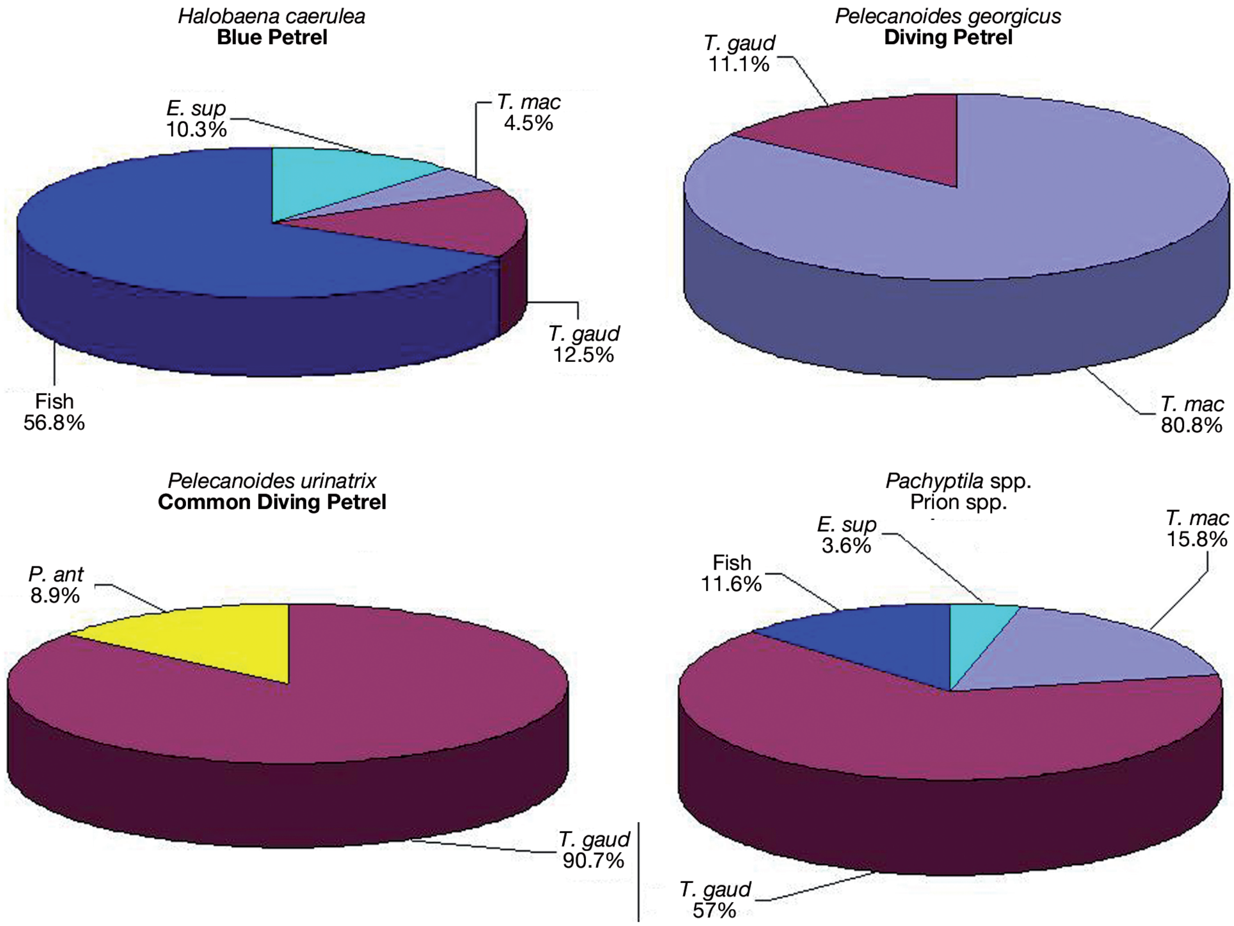

Figure 10. - Stomach content (% mass) of four different species of petrels in Kerguelen during the chicks rearing period. Symbols: *E. sup* = *Euphausia superba*; *T. mac* = *Thysanoessa macrura*; *T. gaud* = *Themisto gaudichaudii*; *P. ant* = *Paraeuchaeta antarctica*.

Diet composition of sea birds

The trophic link between petrels and zooplankton is restricted to the summer period corresponding to the breeding season. Complete information can be found in Bocher *et al*. (2000, 2001, 2002) and Cherel *et al*. (2002a, 2002b) and is summarized here in the context of energy transfer through the Kerguelen food web. All five petrels investigated fed on crustaceans, with four species (diving petrels and prions) being essentially zooplankton feeders (81.9-100.0% by reconstituted mass), but the blue petrel also preyed upon fish (Fig. 10). The main crustacean prey of seabirds was the hyperiid *T. gaudichaudii*, except for the South Georgian diving petrel that fed mainly on *Thysanoessa macrura/vicina*. Some species complemented their diet with copepods: *P. antarctica* (common diving petrel) and *Calanoides acutus* (Giesbrecht, 1902) (South Georgian diving petrel), or presented a more diversified diet suggesting larger foraging areas with complementary food items such as *Euphausia superba* Dana, 1852 (thin-billed and Antarctic prions, blue petrel).

DISCUSSION

The Kerguelen archipelago is relatively unique in the structure and functioning of the food web as it is a clear example of "wasp-waist" type architecture (Cury *et al*., 2000). The food web is strongly regulated by the seasonality of the phytoplankton production with an intensive spring bloom (Razouls *et al*., 1997) and of the zooplankton population of the copepod *D. pectinatus*, which is the main grazer in the island system. Few other species are also present (Razouls *et al*., 1996) and either do not constitute a significant biomass (*Oithona similis* Claus, 1866) or are present at specific periods of the year (*Euphausia vallentini* Stebbing, 1900). The copepod *D. pectinatus* is predated by different planktonic and non planktonic carnivorous species: the copepod *P. antarctica*, the hyperiid *T. gaudichaudii*, euphausiids in summer as well as fish larvae. Island communities are also nursing grounds for various species of micronekton and fish (Labat *et al*., 2005; Koubbi, 1992) fuelling the Kerguelen shelf plankton and fish populations. From a population dynamic

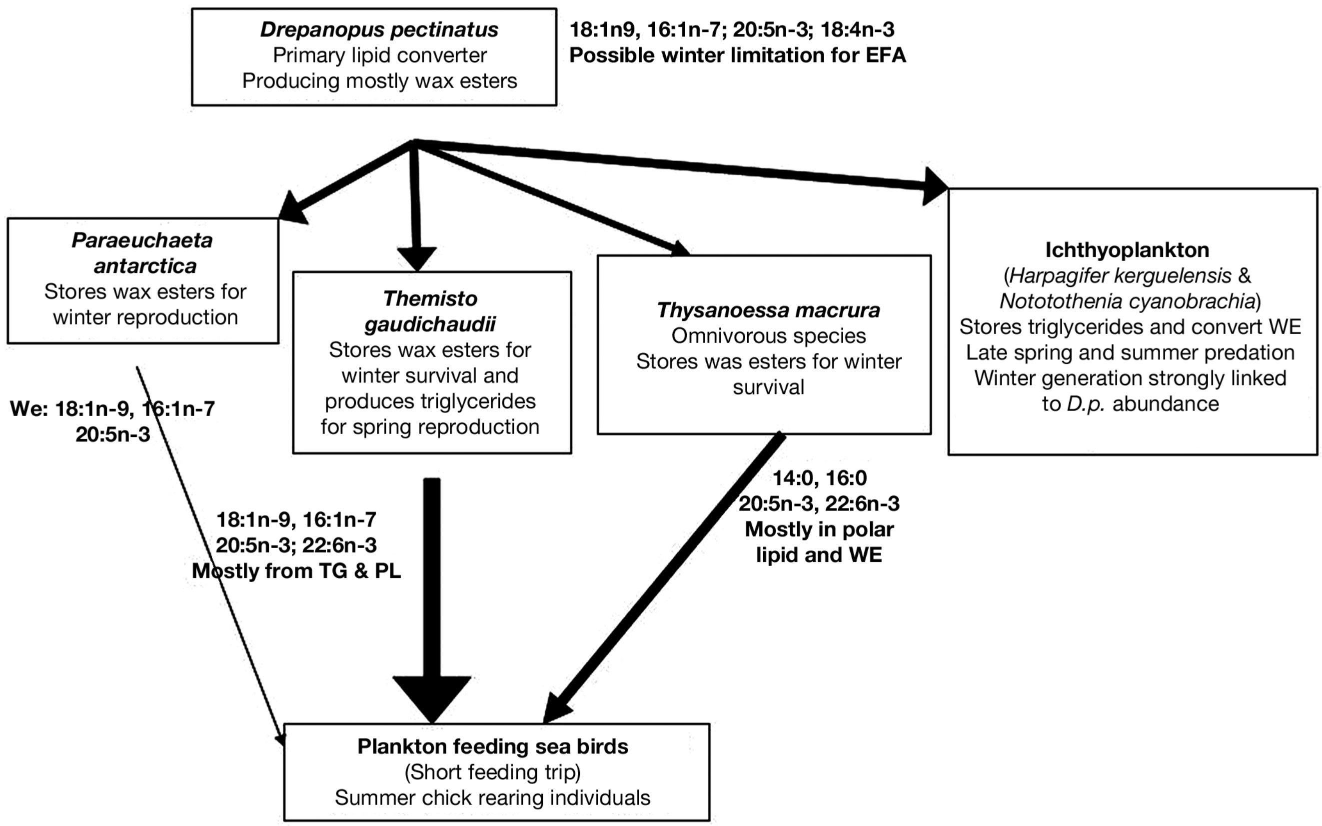

Figure 11. - Lipid and fatty acid flow diagram through the food web of Morbihan Gulf (Kerguelen). Size of arrows illustrates major routes.

point of view, the main constituents of the zooplankton community showed major differences with a shift in time in the reproduction and recruitment processes. Hence, *D. pectinatus* reproduces in summer with recruitment at the same period (Razouls and Razouls, 1988; 1990), while *P. antarctica* reproduces in winter with maximum recruitment in spring and summer (Alonzo *et al*., 2000) and *T. gaudichaudii* reproduces early spring with recruitment late spring-early summer (Labat *et al*., 2005). Little is known on the biological cycle of the euphausiid *Thysanoessa macrura* G.O. Sars, 1983. The species is present inside the Gulf and on the shelf (data not shown) and reproduction is known to take place in spring. Lipid accumulation is essentially as wax esters (Mayzaud *et al*., 2003) but polar lipids remained the main constituent resulting in equal percentages of EPA and DHA.

Such shifts are important from the perspective of trophic interactions and energy transfer. Maximum biomass occurred in spring and summer when the energetic needs of top predators are high. The main prey (*D. pectinatus*) reproduces throughout spring and summer using assimilated phytoplankton as energy source, and maintains high productivity during times of high predation rate. With a winter reproduction based on internal reserves, *P. antarctica* maintains a high biomass of terminal stages (C5 and C6) at a time of low prey availability. The recruitment in spring provides adult stages in summer in phase with higher consumers. The early spring reproduction of *T. gaudichaudii* associated with a late spring protected development and early summer recruitment provides the higher predators with maximum prey availability at times of high requirements (rearing of chicks for seabirds).

Polar zooplankton and especially copepods are known to convert low energy phytoplankton into high energy-lipid rich zooplankton (Falk-Petersen *et al*., 1990), and is the main supplier of energy and essential fatty acids (n-3 PUFA) for higher consumers. The importance of *D. pectinatus* for planktonic carnivores and fish larvae has been illustrated in several studies (Alonzo *et al*., 2003; Mayzaud, unpubl. data) and in the present work. The role of *T. gaudichaudii* and *P. antarctica* as prey for petrels was detailed by Bocher *et al*. (2001; 2002). It is interesting to evaluate the potential availability of lipids and PUFA for the different consumers to obtain a pattern of energy flow through the Morbihan Gulf system in Kerguelen (Fig. 11). *Drepanopus pectinatus* is the primary converter which synthesize essentially wax esters rich in 18:1n-9, 16:1n-7; 20:5n-3 and 18:4n-3. If the predators are not efficient at elongating 20:5 to 22:6 there is a possible winter limitation for essential fatty acids (EFA). Feeding on *D. pectinatus*, *P. antarctica* stores essentially wax esters for winter reproduction with a fatty acid composition quite similar to

that of *Drepanopus*. Hence, it represents an important source of 18:1n-9, 16:1n-7 and 20:5n-3 for higher consumers but a potential limitation in DHA (22:6n-3) if elongation step is limiting. *Themisto gaudichaudii* stores wax esters for winter survival and produces triglycerides for spring reproduction. As a result, its fatty acid pattern derives essentially from the polar lipids and triglycerides with 18:1n-9, 16:1n-7, 20:5n-3 and 22:6n-3 as dominant fatty acids. Similarly, *T. macrura* accumulates wax esters for winter survival but the pattern of PUFA derives essentially from polar lipids with 20:5n-3 and 22:6n-3 in equal proportion associated with saturated acids. Ichtyoplankton (*Harpagifer kerguelensis* Nybelin, 1947 and *Notothenia cyanobrancha*) stores triglycerides and since they feed mostly on *D. pectinatus* during the spring and summer periods, convert wax esters into their own reserves. Winter larvae are strongly linked to *D. pectinatus* and micro-zooplankton abundance. Plankton feeding seabirds were only considered during the summer rearing seasons (Cherel *et al*., 2002a, 2002b). Within the Gulf and on the proximal shelf, their reliance on *T. gaudichaudii* and *T. macrura* supplies a balanced input of fatty acids with both EPA and DHA, which are likely necessary for the growth of the chicks.

In conclusion, despite a very low diversity, the Morbihan Gulf in the Kerguelen Islands and the proximal shelf are an area of high production with maximum biomass standing from mid-spring to late summer because of shifted period in growth and recruitment of the different species. All zooplankters are storing lipids in high quantity to ensure winter survival and/or reproductive requirements. As a result, they are a good food source for higher predators both in quantity and in quality (defined as EFA). Predators tended to feed on the larger size individuals enhancing the energy return per unit capture. If we consider trophic upgrading from phytoplankton as defined by Klein-Breteler *et al*. (1999), low energy phytoplankton with limited percentages of EPA and DHA are transformed by copepods into high lipid content prey with high percentages of either EPA (copepods) or EPA and DHA (hyperiids, euphausiids). More information is needed on the lipid requirements of the predators to complete this global assessment of the efficiency of transfer from primary producers to terminal predators.

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